

Ecological and phytogeographical differentiation of oak-hornbeam forests in southeastern Europe

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Abstract

The aim of the study was to establish the main types of oak-hornbeam (*Carpinus betulus* and *Quercus* sp. div) forests on the Apennines, Balkan peninsula and southern Alps and their correlations with the main ecological and phytogeographical gradients in the region. Furthermore, the comparison with the major types recognized in the traditional expert-based classification was done. 1676 relevés of oak-hornbeam forests (alliances *Erythronio-Carpinion*, *Carpinion moesiicum*, *Physospermo verticillati-Quercion cerris*) from the area of the Apennines, Balkan peninsula and southern Alps were collected and entered in a Turboveg database. 508 relevés remained after stratification and were classified with a Modified Two Way Indicator Species Analysis, which resulted in four main clusters that are phytogeographically interpretable, such as (1) southern Apennines, (2) northern-central and central Apennines, (3) central-southern Balkan and (4) north-western Balkan and southern Alps, further divided into subclusters. Pignatti indicator values calculated for relevés of each subcluster were subjected to PCA in order to show the ecological relationships among subclusters, and the spectra of geo-elements were calculated to show the phytogeographical relationship between them. The diagnostic species combination was calculated by a fidelity measure (phi-coefficient) and presented in a synoptic table. Synsystematic classification of the elaborated groups is proposed.

Key words: *Apennines*, *Balkan peninsula*, *biogeography*, *Carpinus betulus*, *ecological and phytogeographical gradients*, *Quercus sp. div.*, *southern Alps*, *syntaxonomy*

Introduction

The center of distribution of oak-hornbeam forests as zonal vegetation lies in subcontinental areas of east-central Europe and southeastern Europe, in lowlands, hills, and the low mountain belt (Bohn et al. 2003).

In southeastern Europe, the vegetation of oak-hornbeam forests is zonal in the northern part of the Balkan peninsula as far as river the Drina on the southeast and in northern Italy till the Padanian plain. Actually, in the Padanian plain (Po valley) this kind of vegetation was zonal but is now virtually extinct (*Quercus-Carpinetum boreo-italicum* Pignatti 1953 = *Asparago tenuifolii-Quercetum roboris* (Lausi 1966) Marinček 1994). On the Apennines and in the central-southern part of the Balkan peninsula, this

vegetation is extrazonal and is edaphic-oro-graphic conditioned (Kojić et al. 1998; Marinček & Čarni 2000; Biondi et al. 2002, 2008).

In central Europe, these forests are classified into the *Carpinion betuli* alliance (Oberdorfer 1992, Knollová & Chytrý 2004; Willner & Grabherr 2007). For mesophilous deciduous forests of southeastern Europe it has already been established that they differ from forests in central Europe, and vicariant alliances (suballiances) have been described within the order *Fagetalia sylvaticae*. Therefore, the southeastern European alliances *Erythronio-Carpinion* (occurring in the Apennines and Balkans), *Physospermo verticillati-Quercion cerris* (occurring in the southern Apennines) and *Carpinion moesiicum* (occurring in the central-southern Balkans) are vicariant to the central European alliance *Carpinion betuli*

within the order *Fagetalia sylvaticae*. These communities are very rich in species and are characterized by numerous relict and endemic species that survived Quaternary glaciations in southern European refugia (Trinajstić 1992, Bennett et al. 1991; Tzedakis 1993; Magri 1998; Petit et al. 2002). Some of these woods have been considered and recorded as old-growth forests (Blasi et al. 2010; Diaci et al. 2010; Horváth et al. 2012).

There have been some synthetic reviews with attempts at establishing different vegetation types of oak-hornbeam forests in southeastern Europe, but on smaller areas (Biondi et al. 2002, 2008) or without numerical analyses (Marinček & Čarni 2000) and in different taxonomic contexts (Ubaldi 2003).

Numerous researches into forest vegetation in the Apennines and Balkans have been carried out, such as researches on beech forests (Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001; Di Pietro et al. 2004; Tzonev et al. 2006; Tsiripidis et al. 2007), broad-leaved ravine forests (Biondi et al. 2008; Košir et al. 2008) and thermophilous deciduous forests (Blasi et al. 2004; Čarni et al. 2009), in order to establish the major gradients of floristic differentiation of different forest vegetation types in the area. In these investigations, many similarities between the vegetation on both sides of the Adriatic Sea have also been established. In that respect, the question of Apennine and Balkan oak-hornbeam forests and the gradients of their floristic differentiation in the area is raised.

The aim of the study was to establish the main types of oak-hornbeam (*Carpinus betulus* and *Quercus* sp. div) forests on the Apennines, Balkan peninsula and southern Alps and their correlations with ecological and phytogeographical gradients in the region, and to compare them with the major vegetation types recognized in the traditional expert-based classification in order to propose a synsystematic classification of the elaborated groups.

Materials and methods

Study area

Oak-hornbeam forests were studied in the area of the Apennines, Balkan peninsula and southern Alps.

The area is of very complex structure, since it comprises a part of the Pannonian basin, Padanian basin, the coasts of the Mediterranean Sea, southern hillsides of the Alps, the Apennines and various mountain chains in the Balkans.

The research territory is classified into the Euro-Siberian region, above all into the Apennine–Balkan province and also into some adjacent areas of Pannonian–Carpathian provinces, the Adriatic province and Italo–Thyrrhenian province (Rivas-Martinez & Rivas-Saenz 1996–2009).

Object of the research

The objects of the research were oak-hornbeam forests from the area of the Apennines, Balkan peninsula and southern Alps.

The stands are composed mainly of hornbeam (*C. betulus*), and frequently these forests are mixed with other species such as *Q. petraea* and *Q. robur*. In the Apennines and Balkan peninsula, in the stands *Quercus cerris* also appears and sometimes dominates because of forest management. This kind of wood occupies meso- to eutrophic sites, mostly shaded and moderate dry to moist. These stands differ from poor stands of alliance *Quercion robori-petraeae* and from moist and overflowed forests of the alliance *Alnion incanae* (Oberdorfer 1992).

Methods

Forest vegetation relevés made by applying the Braun-Blanquet (1964) approach, classified by their authors into alliances: *Erythronio-Carpinion*, *C. moesiaticum*, *Physospermo verticillati-Quercion cerris*, were collected from the literature, in addition to new and unpublished data. Methodological developments regarding conceptual aspects in accordance with the present state of phytosociology were taken into consideration (Biondi 2011; Biondi et al. 2011; Blasi et al. 2011; Blasi & Frondoni 2011; Feoli et al. 2011; Géhu 2011; Pott 2011; Schaminée et al. 2011).

The relevés with an incomplete list of herb species indicated by the authors were not included into the analyses. We excluded the relevés whose dominant tree species (cover value 4 and 5) are species of other forest types, above all broad-leaved ravine, hygrophilous, coniferous and other climatozonal forests of the area (*Abies alba*, *Acer platanoides*, *A. pseudoplatanus*, *Alnus glutinosa*, *A. incana*, *Carpinus orientalis*, *Fagus sylvatica*, *Fraxinus angustifolia*, *F. excelsior*, *F. ornus*, *Ostrya carpiniifolia*, *Picea abies*, *Pinus* sp. div., *Quercus frainetto*, *Q. ilex*, *Q. pubescens*, *Salix* sp. div., *Tilia platyphyllos*, *Ulmus glabra*), as well as those where none of the tree species characteristic of oak-hornbeam forests (*C. betulus*, *Q. cerris*, *Q. petraea*, *Q. robur*) had a cover value of at least 2 (Chytrý et al. 2002; Košir et al. 2008). We did not include relevés without indication of altitude. As the distinction between these forests and forests of the alliance *Alnion incanae* and the order *Quercetalia robori-petraeae* is sometimes difficult, above all due to similar dominant species, we calculated Pignatti indicator values (Pignatti et al. 2005) for each relevé, so relevés with extreme values of moisture and soil reaction (only when *Quercus* sp. div. dominated the stand) were excluded.

Altogether, 1612 relevés collected from the literature and new ones were entered into the TURBO-VEG (Hennekens & Schaminée 2001) database. After exclusion of the relevés which did not meet the

criteria mentioned above, 1152 relevés remained. This data set was then stratified. Stratified resampling was made by combining the geographical stratification with stratification by phytosociological association (Knollová et al. 2005). This means that up to 10 relevés of one association in one area were selected in such a way that different authors, different publications and different locations within the area were represented. We took the biogeographic map of Europe (Rivas-Martinez & Rivas-Saenz 1996–2009) as the basis for geographical strata. The associations were defined according to expert assignments, and large associations were distinguished on the level of subassociations. After stratification 508 relevés remained.

As many authors did not record mosses, we excluded them from our analysis before numerical processing. For the purpose of numerical analysis, we unified the system of layer division, which differs from author to author in the synoptic table. All layers were merged together into one.

The numerical classification of the vegetation relevés, based on their species composition, was performed with TWINSpan (Hill 1979), using its modified version available in the JUICE program (Tichý 2002). While the classical TWINSpan algorithm divides each cluster coming from the previous division step, the modified algorithm divides only the most heterogeneous cluster in each step. Modification combines the classical TWINSpan algorithm with the analysis of heterogeneity of the clusters prior to each division (Roleček et al. 2009). In such a way, we received successive partitions with 2, 3, 4, 5, etc., clusters, and of these we accept the partition which was effectively interpretable in phytogeographical and ecological terms, based also on authors' suggestions from the literature. Whittaker's beta was used as the heterogeneity measure. TWINSpan pseudospecies cut levels for species abundance were set to 0–2–5–10–20% scale units as proposed by McCune and Grace (2002).

Diagnostic species of each of the eight subclusters and four clusters were determined in the JUICE program (Tichý 2002) by calculating the fidelity of each species to each cluster and subcluster (Bruehlheide 1995, 2000; Chytrý et al. 2002), using the phi-coefficient. In these calculations, each group of relevés was compared with the rest of the relevés in the data set, which were taken as a single undivided group. Each of the eight subclusters and four clusters was virtually adjusted to 1/8 or 1/4 of the size of the entire data set, while holding the percentage occurrences of a species within and outside a target group the same as in the original data set (Tichý & Chytrý 2006). Species with $\phi \geq 30$ were considered as diagnostic for individual subclusters and clusters, but species whose occurrence concentration in the

relevés of a particular cluster or subcluster was not significant at $P < 0.001$ (Fisher's exact test) were excluded. Within the table, species were ordered by decreasing fidelity to individual clusters, i.e. by their decreasing diagnostic value. Since the diagnostic species are calculated on the basis of a data set of oak-hornbeam forests of southeastern Europe, they are only used for the purpose of differentiating the stands within these kinds of forests (Knollová & Chytrý 2004).

Species in tree layer that appear in at least 50% of relevés of an individual cluster and subcluster are treated as constant.

For further interpretation of the eight subclusters, unweighted average indicator values for relevés of the eight subclusters (Pignatti et al. 2005) calculated in the JUICE program and altitude values were presented with Box-whiskers diagrams made in the STATISTICA program (STATSOFT inc. 2007). Unweighted average indicator values and average altitude values for relevé subclusters were also passively projected onto a Principal Components Analysis biplot (PCA from CANOCO 4.5; Ter Braak & Šmilauer 2002) to show ecological relationships among these subclusters and to explain environmental gradients underlying the main ordination axes. Square-root transformed percentage frequencies were used as the input data.

We also calculated the spectra of geo-elements of individual subclusters. Spectra of geo-elements were calculated according to Pignatti et al. (2005). In general, the categories of geo-elements proposed by Pignatti et al. (2005) were taken into consideration, but some adjustments were made, such as Apennine endemic, Stenomediterranean, Eurymediterranean, Mediterranean-montane (incorporating montane S European), Eurasian, separately elaborating SE European (incorporating montane SE European) and Pontic, Atlantic (incorporating montane SW-European), Eurosiberian and Cosmopolite (incorporating Paleotropic and Adventive, Cultivated).

In the calculations, we considered only species occurring in at least three relevés within an individual subcluster (Dzwonko et al. 1999; Košir et al. 2008). The spectra of geo-elements are presented as proportions (percentage) of the entire species composition of individual subclusters and indicated at the head of the synoptic table to show horological features of the subclusters.

The nomenclature is according to Flora Europaea (Tutin et al. 1964–1980), except *Acer neapolitanum* Ten., *Festuca exaltata* C. Presl. and *Pulmonaria apennina* Cristof. & Puppi. *Fagus moesiaca* (K. Malý) Czeczott has been considered as *Fagus sylvatica* L. subsp. *moesiaca* (K. Malý) Szafer and therefore merged with *F. sylvatica* L. subsp. *sylvatica* into taxon *F. sylvatica* L. (Gömöry et al. 1999). The taxon

Quercus virgiliana (Ten.) Ten. is treated as *Quercus pubescens* s.l. (Škvorc et al. 2005).

Results

Clusters and their interpretation

Figure 2 shows the result of the TWINSpan classification of the data set, revealing eight groups of relevés that are ecologically and phytogeographically interpretable. In the first division of the TWINSpan classification, Apennine forests (clusters 1 and 2) were separated from the Balkan and southern Alps forests (clusters 3 and 4).

Apennine forests were further divided into two clusters; south Apennine forests (cluster 1) and northern-central and central Apennine forests (cluster 2).

The Balkan and southern Alps forests were divided into two clusters; central-south Balkan forests (cluster 3), further divided into three subclusters according to their phytogeographical position (3.1 – lowland pannonian, 3.2 – hilly pannonian and 3.3 – montane central-south Balkan forests), and north-west Balkan forests (cluster 4), further divided into three subclusters according to ecology and phytogeography (4.1 – azonal moist *Quercus robur* forests, 4.2 – submediterranean and prealpine basiphilous forests and 4.3 – subpannonian and predinaric moderate acidophylous forests).

Cluster 1. This corresponds to subcluster 1.1 and is represented exclusively by oak-hornbeam forests from the southern Apennines (Figure 1; sectors 21a, 20d). They are moderately acidophilous, thriving on the warmest and driest sites (Figure 3). Constant species in the tree layer are: *C. betulus*, *Q. cerris*, *A. neapolitanum* and *Sorbus torminalis*. These forests correspond to the alliance *Physospermo verticillati-Quercion cerris* (Biondi et al. 2008).

The cluster is characterized by species indicating the phytogeographical position of the relevés in the south of the Apennines (*Doronicum orientale*, *Anemone apennina*, *A. neapolitanum*, *F. exaltata*, *Physospermum verticillatum*, *Lathyrus niger* subsp. *jordanii*, *Viola odorata*, etc.) and also by mesophilous elements of the submontane belt that are widespread in all of the southern area (*Anthriscus nemorosa*, *Corydalis cava*, *Ilex aquifolium*, *Scilla bifolia*, *Arum orientale* subsp. *luca-num*) and thermophilous species (*Asparagus acutifolius*, *Erica arborea*, *Ruscus aculeatus*, *Quercus ilex*, *Rosa sempervirens*) showing that these forests are in contact with evergreen forests of *Quercetia ilicis*.

Cluster 2. This corresponds to subcluster 2.1 and is represented by relevés from the northern-central and central Apennines (Figure 1; sector 9a). They thrive

at highest altitudes with an average altitude value of 850 m and on sites with the highest indicator value of light (Figure 3). Constant species in the tree layer are *Quercus cerris*, *Acer campestre* and *C. betulus*. They were traditionally classified into the suballiance *Pulmonario apenninae-Carpinenion betuli* of the alliance *Erythronio-Carpinion* (Biondi et al. 2002, 2006, 2010).

Both clusters (clusters 1 and 2) are represented by mesophilous forests dominated by *C. betulus* or *Q. cerris* that thrive on the Apennines from the northern-central part to the south. These forests are often remnants of ancient wide forests and worthy of preservation according to Directive 92/43/EEC (European Commission 2007, Biondi et al. 2009). Unfortunately, they are dispersed in highly degraded areas and for this reason it is necessary to create ecological corridors that integrate, according to the Pan European Landscape Strategy (Council of Europe 1996), the areas with the greatest concentration of habitats sensu Directive 92/43/EEC as proposed in Biondi et al. (2012).

Diagnostic species common for both clusters that comprise relevés from the Apennines are indicated in Table I: *Daphne laureola*, *Pulmonaria apennina*, *Viola alba* subsp. *dehnhardtii*, *Q. cerris* and *Lilium bulbiferum* subsp. *croceum*. In comparison to the forests of the Balkan peninsula, the amount of Mediterranean species is higher in the Apennine forests, while the participation of Eurasian and SE-European species is lower. There are also some endemic species in the Apennine forests that separate these forests from the forests of the Balkan peninsula.

Cluster 3. This is represented by central-south Balkan forests (Figure 1; sectors 9c-southeastern part, 10 a). They have the most continental character (Figure 3), as is also indicated by diagnostic species (Table I) such as *Acer tataricum* and *Tilia tomentosa* (both pontic species). Constant species in the tree layer are *C. betulus*, *A. campestre*, and *Q. petraea*. These forests were traditionally classified in the suballiance *Lonicero-Carpinenion* of the alliance *Erythronio-Carpinion* and in the alliance *C. moesiicum*.

The proportion of Mediterranean-montane species is considerably lower in this cluster in comparison with all other clusters (Table I) and the proportion of pontic species is higher, which is all in accordance with the geographical position of the relevés. Except for subcluster 3.1, the proportion of SE-European species is also relatively high.

Subcluster 3.1. This is exclusively represented by forests from the pannonian sector of the Pannonian-Carpathian provinces close to the Illyrian sector (Figure 1; sector 10a; eastern Slavonia, Mecsek, Vršacke planine, Šumadija), as is also indicated by

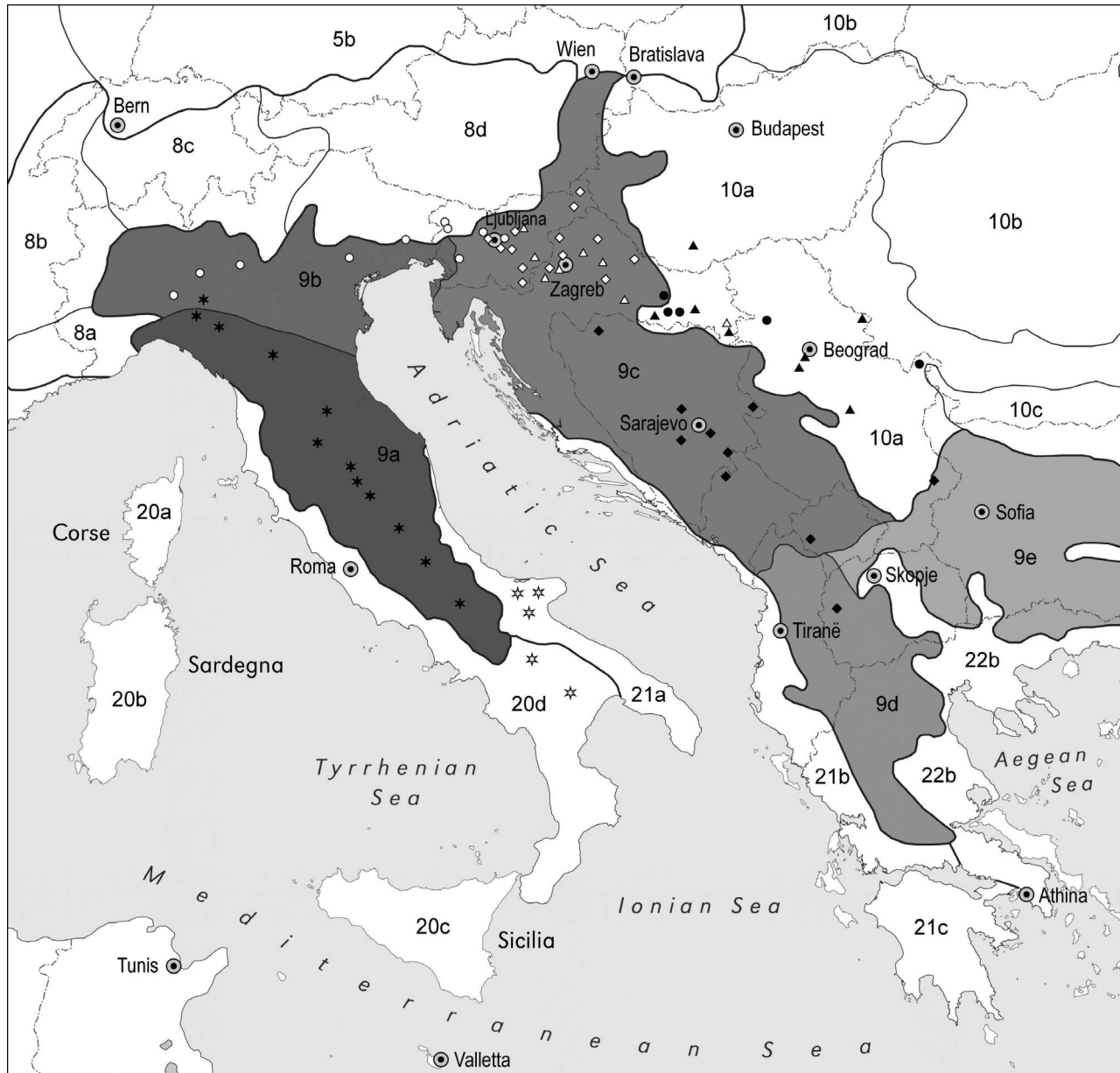


Figure 1. The study area on the Biogeographical map of Europe (Rivas-Martinez & Rivas-Saenz 1996–2009) with the location of relevés, included in the analyses.

Legend: The Apennine-Balkan province (9; shaded) with the Apennine (9a), Padanian (9b), Illyrian (9c), Pindan (9d) sectors, Alpine province (8) with Eastern Alpine sector (8d), Pannonian-Carpathian province (10) with the Pannonian sector (10a), Adriatic province (21) with the Apulian sector (21a) and Italo-Thyrrhenian province (20) with the Coastal west Italian sector (20d). Oak-hornbeam forests recognized in this paper:

alliance: *Physospermo verticillati-Quercion cerris*

| *Physospermo verticillati-Quercion cerris* (Subcluster 1.1 in Table 1),

[*Pulmonario apenninae-Carpinenion betuli* (Subcluster 2.1 in Table 1),

alliance: *Erythronio-Carpinion*:

♂ *Aceri tatarici-Carpinenion betuli* (Subcluster 3.1 in Table 1),

● *Aceri tatarici-Carpinenion betuli* (Subcluster 3.2 in Table 1),

◆ *Aceri tatarici-Carpinenion betuli* (Subcluster 3.3 in Table 1),

B *Lonicero-Carpinenion betuli* (Subcluster 4.1 in Table 1),

○ *Lonicero-Carpinenion betuli* (Subcluster 4.2 in Table 1),

◇ *Lonicero-Carpinenion betuli* (Subcluster 4.3 in Table 1).

the lower proportion of SE-European species in comparison with the other two subclusters of this cluster. They are the most thermophilous and the most continental, thriving at low altitudes around

250 m (Figure 3). Constant species in the tree layer are *C. betulus*, *Q. petraea*, and *T. tomentosa*.

The subcluster is characterized by a group of thermophilous and nitrophilous species with

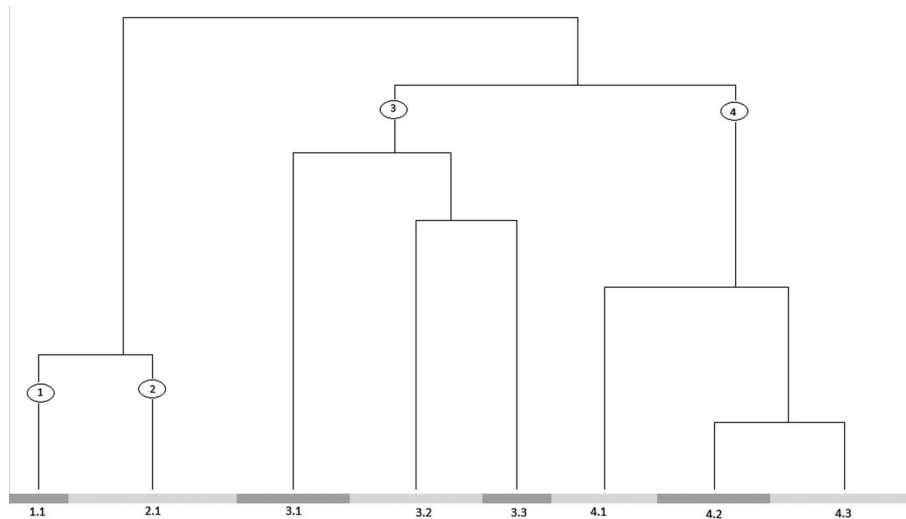


Figure 2. Dendrogram of TWINSpan classification of oak-hornbeam forests of Apennines, Balkan peninsula and southern Alps. See also Supplementary material.

Eurasian distribution (Table I; *Lamium maculatum*, *Galium aparine*, *Alliaria officinalis*), and also by species with pontic (*T. tomentosa*), and SE-European (*Helleborus odorus*, *Glechoma hirsuta*, *Q. frainetto*) distribution.

Subcluster 3.2. This is represented by forests from hilly areas in the scattered islands of Illyrian vegetation within the Pannonian-Carpathian province, mainly from the areas of Slavonko Gorje and Fruška Gora (Figure 1; sectors 9c, 10a) at slightly higher altitudes than forests of subcluster 3.1 (Figure 3). It is characterized by species indicating the transitional character of stands towards *F. sylvatica* forests such as *Lathyrus vernus* and *Ruscus hypoglossum*. Constant species in the tree layer are *C. betulus*, *Q. petraea*, and *F. sylvatica*.

Subcluster 3.3. This is represented by montane central-south Balkan forests (Figure 1; sectors 9c, 9d, 9e; Bosnia and Herzegovina, south Serbia, Montenegro and Macedonia). They thrive at the highest altitudes among Balkan oak-hornbeam forests with an average altitude around 640 m (Figure 3). Diagnostic species indicate the geographical position of the relevés in the south of Balkans (*Physospermum cornubiense*, *Coronilla elegans*), on deep and acidic soils (*Chamaespartium sagittale*, *Danthonia decumbens*, *Potentilla erecta*) and there are also thermophilous species such as *Hieracium praealtum* subsp. *bauhinii* that reflect the global climate. Constant species in the tree layer are *C. betulus* and *Q. petraea*.

Cluster 4. This is represented by forests of the northwest Balkans, predominantly of the north-western part of the Illyrian sector, but including also

the Padanian sector and the Eastern-Alpine sector (Figure 1; sectors 9c, 9b, 8d). These forests traditionally correspond to the pre-Alpine and west pre-dinaric suballiance *Erythronio-Carpinenion*, the submediterranean suballiance *Asparago tenuifolii-Carpinenion* and partly (northwestern part) to the subpannonian Illyrian suballiance *Lonicero caprifoliae-Carpinenion*. Forests of this cluster thrive on the moistest, coldest and shadiest sites (Figure 3), which is in accordance with their geographical position on the northern part of the research area. Species with Eurosiberian distribution are well represented. Except for subcluster 4.1 (azonal *Q. robur* forests), the proportion of SE-European species is relatively high.

Forests of this cluster are characterized by Illyrian species, i.e. relic endemics of mesophilous forests sites of southeastern distribution, including *Aposeria foetida*, *Cyclamen purpurascens*, *Crocus vernus*, *Knautia drymeia*, *Lamium orvala*, *Hacquetia epipactis*, and also by other species indicating the mesophilous character of the stands (Table I, e.g. *Anemone nemorosa*, *P. abies*). Constant species in the tree layer are *C. betulus* and *Q. petraea* agg.

Subcluster 4.1. This is represented by azonal *Q. robur* forests of the area of the Illyrian sector (Figure 1; sector 9c). The relatively high proportion of cosmopolite species and low proportion of SE-European species indicate the azonal character of these stands. Forests of this cluster thrive at lowest altitudes, they are acidophilous, nitrophilous and the most humid (Figure 3). This ecology is reflected also in the diagnostic species (Table I, e.g. *Q. robur*, *Carex brizoides*, *Pseudostellaria europaea*). Constant species in the tree layer are *C. betulus* and *Q. robur*.

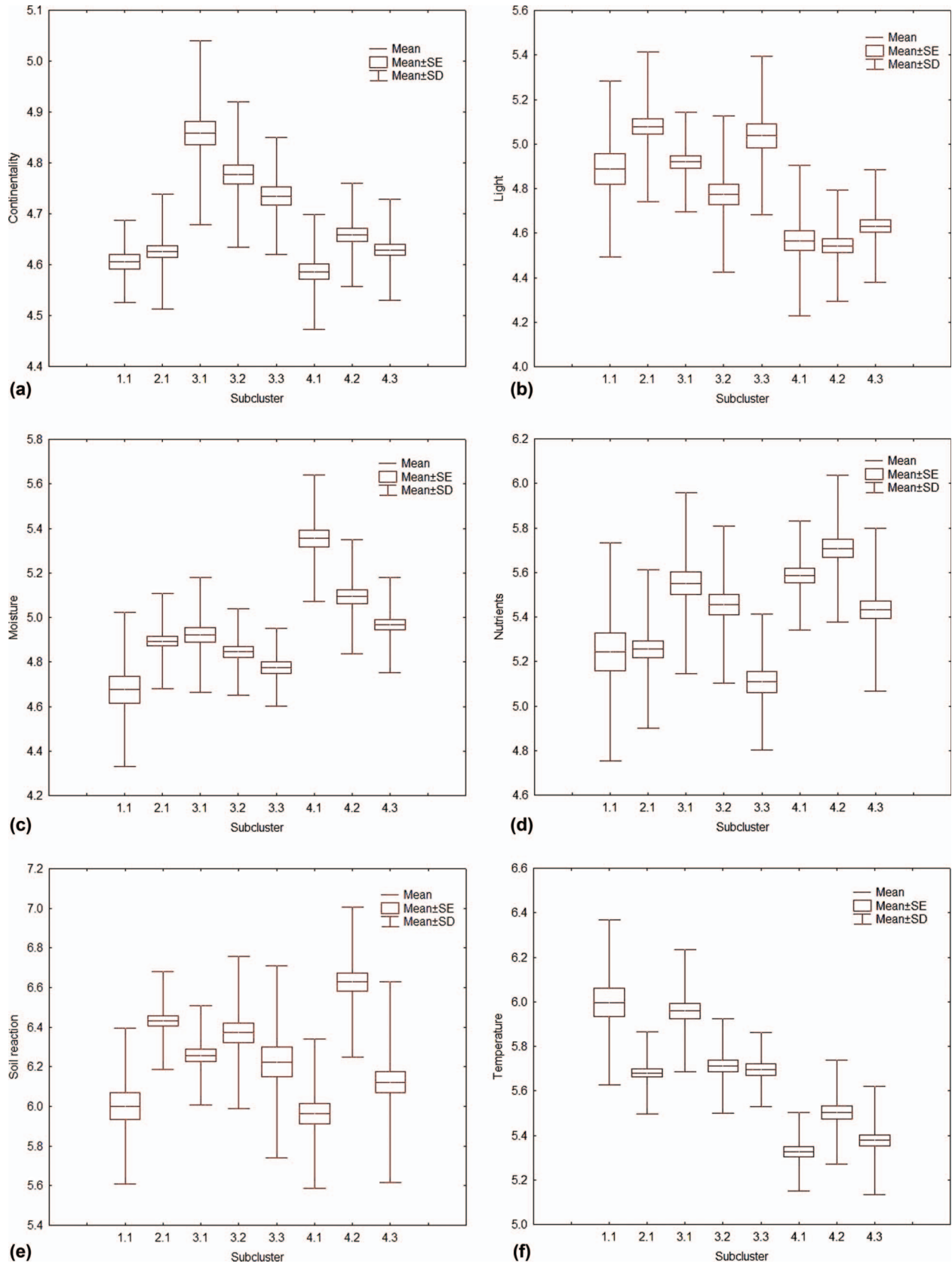


Figure 3. Relationships of the eight main forest types of the Apennines, Balkan peninsula and southern Alps to Pignatti indicator values (a–f) and altitude (g). Boxes represent mean and standard errors (SE), whiskers indicate standard deviations (SD). Subclusters are numbered as in Figure 2.

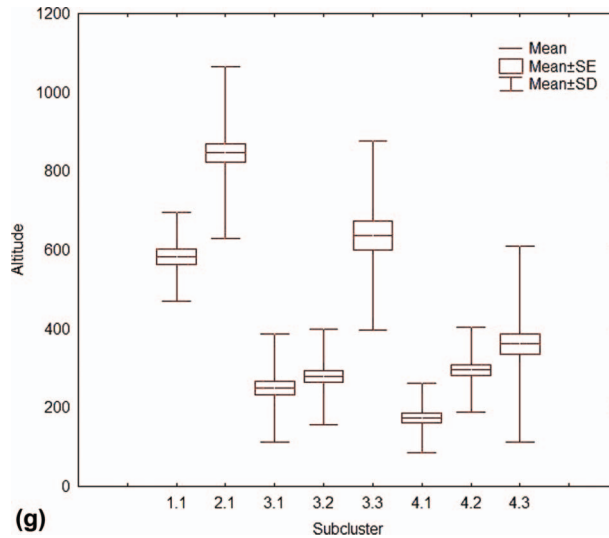


Figure 3. (Continued)

Subcluster 4.2. This represents the basiphilous zonal forests of the western part (pre-Alpine and submediterranean) of the northwest Illyrian sector, including also forests of the Padanian and Eastern-Alpine sector (Figure 1; sectors 9c, 9b, 8d). These forests thrive on shallow soils over carbonate bedrock (predominantly limestone) rich in nutrients; they are the most basiphilous ones (Figure 3). This subcluster is characterized by numerous Illyrian species. Diagnostic species (Table I, e.g. *Anemone trifolia*, *Carex alba*, *C. purpurascens*, *H. epipactis*, *L. orvala*, *Mercurialis perennis*, *Omphalodes verna*) indicate the geographical position in the pre-Alpine and submediterranean area of the northwest Balkans and the basiphilous character of the stands. Constant species in the tree layer are *C. betulus* and *Acer campestre*.

Subcluster 4.3. This is represented by neutrophilous and moderate acidophilous forests predominantly of the eastern part (pre-Dinaric, subpannonian) of the northwest Illyrian sector (Figure 1; sector 9c) which thrive on deeper soils poor in carbonate; on sandstones, clay, loam or non-calcareous flysch, and also on deeper soils over carbonate bedrock. The subcluster is characterized by moderate acidophilous species such as *Gentiana asclepiadea*, *Castanea sativa*, *Luzula luzuloides*, *Serratula tinctoria*, *Hieracium racemosum* and others (Table I). Constant species in the tree layer are *C. betulus*, *Q. petraea* agg, and *F. sylvatica*.

Indicator values and altitude value

The PCA is presented of the eight subclusters of oak-hornbeam forests of the research area with mean Pignatti indicator values and altitude plotted as supplementary variables on the ordination diagram

(Figure 4). Eigenvalues of the first two axes are 0.377 and 0.172.

Oak-hornbeam forests of the research area are separated along axis 1 according to phytogeography, similarly as in the TWINSpan classification (Figure 2; four compartments corresponding to four clusters in the TWINSpan classification). The underlying ecological gradients of axis 1 are temperature, altitude, moisture, light and nutrient, which all reflect different climates of the different phytogeographical regions. Along axis 2, forests are separated according to altitude and soil reaction (Figure 4). Continentality is only correlated with axis 3 and therefore not shown on the PCA diagram.

Discussion

Gradients and classification

The TWINSpan classification reflects both the ecological and phytogeographical gradients that are sometimes difficult to separate as the differences in geographical position that result from different macroclimatic and geological conditions are always reflected together with ecological ones.

The first division separates the Apennine forests from the Balkan and southern Alps forests. The vegetations of the Apennines and Balkans share a part of their history and therefore similar species composition, but there are also differences in species composition between both peninsulas because of the different climate and therefore ecology of these forests.

The first four groups (second level of division) correspond to the main phytogeographical groups: (1) southern Apennines, (2) northern-central and central Apennines, (3) central-southern Balkans and (4) north-western Balkans and southern Alps.

Table I. Synoptic table of species occurrence (percentage frequency) in the eight main forest types of oak-hornbeam forests in southeastern Europe resulting from the TWINSPAN classification (see also Supplementary material).

Subcluster number	1.1	2.1	3.1	3.2	3.3	4.1	4.2	4.3
No. of relevés	33	93	64	62	43	57	65	91
Cluster number	1	2	3			4		
Proportion of geo-elements in clusters (%)								
Apennine endemic	4.92	1.97	0.61				0.52	
Stenomediterranean	12.3	3.45	1.23	1.52	1.76		1.05	0.99
Eurymediterranean	13.93	8.37	7.36	7.58	5.88	5.37	3.66	5.45
Mediterranean-montane	4.1	4.93	2.45	1.52	2.94	4.62	4.19	4.95
Pontic	4.1	8.37	9.82	8.33	11.18	3.85	5.24	5.94
Eurasian	44.26	47.78	56.44	58.33	51.76	58.46	51.83	53.47
SE-European	3.28	4.43	3.68	6.06	7.06	4.62	7.85	6.93
Eurosiberian	7.38	12.81	13.5	10.61	13.53	17.69	17.8	18.32
Atlantic	2.46	3.94			2.35		2.62	
Cosmopolite	2.46	3.94	4.29	4.55	2.94	5.38	4.71	2.97
Species diagnostic for one cluster								
Cluster 1								
<i>Doronicum orientale</i>	88*	–	2	–	–	–	–	–
<i>Anemone apennina</i>	91*	6	–	–	–	–	–	–
<i>Acer neapolitanum</i>	64*	–	–	–	–	–	–	–
<i>Ilex aquifolium</i>	73*	12	–	2	5	–	–	10
<i>Festuca exaltata</i>	48*	–	–	–	–	–	–	–
<i>Teucrium scordonia</i> subsp. <i>euganeum</i>	52*	6	–	–	–	–	–	–
<i>Allium pendulinum</i>	45*	1	–	–	–	–	–	–
<i>Ruscus aculeatus</i>	85*	10	52	24	7	14	28	13
<i>Cyclamen hederifolium</i>	58*	26	–	–	19	–	–	–
<i>Physospermum verticillatum</i>	36*	–	–	–	–	–	–	–
<i>Cyclamen repandum</i>	39*	4	–	–	–	–	–	–
<i>Carex hallerana</i>	36*	1	–	–	–	–	–	–
<i>Erica arborea</i>	30*	–	–	–	–	–	–	–
<i>Lathyrus niger</i> subsp. <i>jordanii</i>	30*	–	–	–	–	–	–	–
<i>Quercus ilex</i>	30*	1	–	–	–	–	–	–
<i>Viola odorata</i>	42*	9	14	3	–	–	–	–
<i>Sorbus domestica</i>	36*	11	–	3	–	–	–	–
<i>Cytisus villosus</i>	33*	10	–	–	–	–	–	–
<i>Ranunculus lanuginosus</i>	48*	20	5	–	2	4	14	15
<i>Rosa sempervirens</i>	21*	–	–	–	–	–	–	–
<i>Scilla bifolia</i>	36*	6	6	–	7	–	18	3
<i>Arum italicum</i>	21*	3	–	–	–	–	–	–
<i>Poa trivialis</i>	21*	6	–	–	–	–	–	–
<i>Buglossoides purpureoerulea</i>	30*	9	5	–	21	–	3	–
<i>Tamus communis</i>	55	37	16	18	9	7	8	21
<i>Rubus caesius</i>	45	28	6	2	–	21	22	3
<i>Crepis leontodontoides</i>	15*	–	–	–	–	–	–	–
<i>Rubia peregrina</i>	15*	–	–	–	–	–	–	–
<i>Asphodelus aestivus</i>	15*	–	–	–	–	–	–	–
<i>Anthriscus nemorosa</i>	15*	–	–	–	–	–	–	–
<i>Geranium sanguineum</i>	15*	–	–	–	–	–	–	–
<i>Potentilla micrantha</i>	45	29	3	29	7	9	–	14
<i>Sorbus torminalis</i>	55	19	8	39	42	2	6	31
<i>Sanicula europaea</i>	73	44	16	29	56	33	17	53
<i>Rosa canina</i>	27	12	3	8	12	–	–	1
<i>Bellis sylvestris</i>	12*	–	–	–	–	–	–	–
<i>Arum orientale</i> subsp. <i>lucanum</i>	12*	–	–	–	–	–	–	–
Cluster 2								
<i>Acer obtusatum</i>	–	42*	–	2	9	–	–	–
<i>Festuca heterophylla</i>	42	67*	2	2	40	–	20	19
<i>Rosa arvensis</i>	33	76*	22	8	35	4	29	36
<i>Geranium nodosum</i>	–	38*	–	–	7	4	15	–
<i>Luzula forsteri</i>	30	40*	2	2	16	–	–	2
<i>Juniperus communis</i>	–	29*	–	2	5	–	–	5
<i>Dactylorhiza fuchsii</i>	3	23*	–	–	–	–	2	–
<i>Lathyrus venetus</i>	45	49*	23	3	30	–	8	–
<i>Helleborus bocconei</i>	–	19*	–	–	–	–	–	–

(continued)

Table I. (Continued)

Subcluster number	1.1	2.1	3.1	3.2	3.3	4.1	4.2	4.3
<i>Lonicera caprifolium</i>	3	56*	17	13	23	5	15	27
<i>Melica uniflora</i>	64	70*	34	42	44	16	6	13
<i>Euonymus latifolius</i>	–	22*	–	–	5	–	2	1
<i>r Primula vulgaris</i>	–	73	23	13	51	5	83*	40
<i>Prunus spinosa</i>	27	39	14	5	23	7	2	5
<i>Platanthera chlorantha</i>	–	14*	–	–	–	–	–	–
<i>Bromus ramosus</i> agg.	9	24*	11	–	–	–	2	1
<i>Digitalis lutea</i> subsp. <i>australis</i>	12	15	–	–	–	–	–	–
<i>Crataegus laevigata</i>	–	49	27	5	5	44	22	18
<i>Astragalus glycyphyllos</i>	6	23	3	2	14	–	3	1
<i>Lonicera xylosteum</i>	9	38	–	11	7	–	42	7
Cluster 3								
<i>Helleborus odorus</i>	–	1	64*	32	42	–	22	1
<i>Tilia tomentosa</i>	–	–	69*	37	2	4	–	7
<i>Acer tataricum</i>	–	–	28	39*	33	2	–	1
<i>Glechoma hirsuta</i>	–	1	36*	29	7	–	3	7
Cluster 4								
<i>Anemone nemorosa</i>	–	13	8	2	21	65	65	66
<i>Aposeris foetida</i>	–	–	–	–	14	7	51*	59*
<i>Cyclamen purpurascens</i>	–	–	–	3	5	2	51*	34
<i>Crocus vernus</i>	6	1	–	–	5	19	45*	29
<i>Gentiana asclepiadea</i>	–	–	–	–	5	25	3	46*
<i>Luzula pilosa</i>	–	–	–	10	9	47*	17	41
<i>Lamium orvata</i>	–	–	–	2	5	7	46*	26
<i>Oxalis acetosella</i>	–	–	5	16	5	58*	35	26
<i>Vinca minor</i>	–	3	5	5	7	16	62*	25
<i>Athyrium filix-femina</i>	–	–	6	19	5	72*	11	34
<i>Daphne mezereum</i>	–	–	–	–	7	11	22	32*
<i>Picea abies</i>	–	–	–	–	2	12	31*	18
<i>Hacquetia epipactis</i>	–	–	–	2	–	–	42*	16
<i>Euphorbia dulcis</i>	–	35	–	6	12	42	45	56
<i>Maianthemum bifolium</i>	–	–	–	2	–	32*	8	13
<i>Robinia pseudacacia</i>	–	–	2	3	2	4	40*	14
<i>Knautia drymeia</i>	–	8	2	13	9	12	29	47*
<i>Carex digitata</i>	15	3	2	5	12	5	52*	30
<i>Carex brizoides</i>	–	–	2	5	–	54*	–	8
<i>Lamium galeobdolon</i>	–	6	31	35	12	70*	48	35
Species diagnostic for more than one cluster								
<i>Daphne laureola</i>	70*	66*	–	–	16	–	2	1
<i>Pulmonaria apennina</i>	64*	55*	–	–	–	–	–	–
<i>Viola alba</i> subsp. <i>denhardtii</i>	61*	39*	–	–	–	–	–	–
<i>Quercus cerris</i>	73	85*	52	24	30	2	15	10
<i>Lilium bulbiferum</i> subsp. <i>Croceum</i>	33*	30*	–	–	–	–	3	–
Species diagnostic for one subcluster								
<i>Asparagus acutifolius</i>	12*	1	–	–	–	–	–	–
<i>Cardamine graeca</i>	12*	1	–	–	–	–	–	–
<i>Lamium maculatum</i>	12	–	44*	3	5	7	–	–
<i>Galium aparine</i>	15	9	50*	5	2	4	2	4
<i>Alliaria officinalis</i>	12	2	41*	3	–	2	6	3
<i>Dactylis glomerata</i> subsp. <i>aschersoniana</i>	–	1	23*	–	2	2	2	1
<i>Veronica hederifolia</i>	18	–	22*	–	–	–	–	–
<i>Geranium robertianum</i>	9	27	48*	11	9	4	11	1
<i>Stachys sylvatica</i>	3	3	27*	5	2	2	5	2
<i>Ranunculus ficaria</i>	39	1	48*	2	2	25	18	14
<i>Ranunculus cassubicus</i> s.lat.	–	–	11*	–	–	–	–	–
<i>Quercus frainetto</i>	3	–	14*	–	2	–	–	–
<i>Rosa species</i>	–	–	9	26*	7	2	6	–
<i>Lathyrus vernus</i>	–	9	22	63*	21	18	40	31
<i>Ruscus hypoglossum</i>	–	2	9	29*	–	4	–	11
<i>Coronilla elegans</i>	–	–	–	–	19*	–	–	–
<i>Hieracium praealtum</i> subsp. <i>bauhinii</i>	–	–	–	–	19*	–	–	–
<i>Chamaespartium sagittale</i>	–	1	–	–	19*	–	–	–
<i>Vicia cracca</i>	–	1	–	–	16*	–	–	–

(continued)

Table I. (Continued)

Subcluster number	1.1	2.1	3.1	3.2	3.3	4.1	4.2	4.3
<i>Danthonia decumbens</i>	–	–	–	–	14*	–	–	–
<i>Physospermum cornubiense</i>	–	2	–	–	19*	–	5	–
<i>Pyrus pyraaster</i>	3	32	16	19	63*	18	8	32
<i>Potentilla erecta</i>	–	–	–	–	16*	–	–	4
<i>Quercus robur</i>	–	4	28	15	9	89*	18	10
<i>Galeopsis tetrahit</i>	–	3	9	8	2	49*	–	3
<i>Pseudostellaria europaea</i>	–	–	–	–	–	19*	–	1
<i>Gagea spathacea</i>	–	–	–	–	–	16*	–	–
<i>Circaea lutetiana</i>	–	4	16	31	–	51*	2	13
<i>Veronica montana</i>	18	3	9	8	–	30*	–	1
<i>Scrophularia nodosa</i>	–	2	8	11	5	39*	3	21
<i>Carex remota</i>	–	1	8	–	–	19*	–	1
<i>Anemone trifolia</i>	–	19	–	3	5	–	54*	3
<i>Carex alba</i>	–	–	–	2	–	–	23*	–
<i>Fraxinus excelsior</i>	–	5	8	2	9	2	40*	3
<i>Omphalodes verna</i>	–	–	–	–	2	–	25*	3
<i>Colchicum autumnale</i>	–	–	–	–	–	–	20*	2
<i>Hepatica nobilis</i>	–	44	12	16	12	–	62*	10
<i>Asplenium scolopendrium</i>	6	–	–	–	2	–	18*	–
<i>Lathraea squamaria</i>	–	–	5	–	–	4	26*	7
<i>Salvia glutinosa</i>	–	25	–	6	14	–	51*	25
<i>Melica nutans</i>	–	–	6	2	5	2	34*	18
<i>r Primula vulgaris</i>	–	73	23	13	51	5	83*	40
<i>Helleborus viridis</i>	–	–	–	2	–	2	15*	–
<i>Galanthus nivalis</i>	24	8	27	3	7	5	46*	10
<i>Mercurialis perennis</i>	18	6	25	6	21	7	48*	10
<i>Asarum europaeum</i>	–	16	27	48	33	26	78*	58
<i>Helleborus multifidus</i> subsp. <i>istriacus</i>	–	–	–	–	–	–	11*	–
<i>Luzula luzuloides</i>	–	–	–	5	19	9	2	35*
<i>Castanea sativa</i>	12	12	–	3	14	11	20	51*
<i>Serratula tinctoria</i>	–	9	–	2	7	2	9	35*
<i>Hieracium racemosum</i>	6	4	–	3	2	9	3	32*
<i>Quercus petraea</i> agg.	3	15	61	85	84	23	51	96*
<i>Molinia arundinacea</i>	–	–	–	–	–	–	–	11*
<i>Convallaria majalis</i>	–	–	8	3	9	7	12	32*
<i>Solidago virgaurea</i>	–	22	–	–	14	5	18	42*
Species diagnostic for more than one subclusters								
<i>Corydalis cava</i>	36*	–	31*	–	–	2	12	4
<i>Pteridium aquilinum</i>	67*	35	–	10	33	11	5	63*
Other species with high frequency								
<i>Carpinus betulus</i>	76	80	100	97	100	100	100	99
<i>Acer campestre</i>	64	82	86	79	72	47	86	44
<i>Viola reichenbachiana</i>	61	71	48	42	70	51	60	63
<i>Crataegus monogyna</i>	76	61	66	56	70	26	55	41
<i>Hedera helix</i>	88	77	53	47	33	21	69	58
<i>Corylus avellana</i>	–	63	16	39	72	58	85	75
<i>Fagus sylvatica</i>	33	48	25	79	56	46	31	68
<i>Rubus fruticosus</i> agg.	55	41	27	85	28	53	17	66
<i>Pulmonaria officinalis</i>	–	8	55	47	74	44	78	59
<i>Fragaria vesca</i>	58	60	38	24	67	30	28	52
<i>Prunus avium</i>	3	30	45	68	51	32	45	74
<i>Euphorbia amygdaloides</i>	58	44	48	52	70	23	20	15
<i>Polygonatum multiflorum</i>	36	17	34	37	16	63	55	56
<i>Cornus sanguinea</i>	3	45	34	56	35	30	58	43
<i>Carex sylvatica</i>	45	33	23	39	21	61	22	57
<i>Brachypodium sylvaticum</i>	58	44	30	16	49	19	45	35
<i>Fraxinus ornus</i>	24	45	41	52	51	–	40	37
<i>Stellaria holostea</i>	9	12	41	60	53	46	11	48
<i>Geum urbanum</i>	61	45	59	31	33	21	11	3
<i>Euonymus europaeus</i>	36	34	34	26	12	33	51	32
<i>Symphytum tuberosum</i>	–	16	17	21	53	33	69	46
<i>Galium odoratum</i>	36	15	27	47	23	49	6	47
<i>Ajuga reptans</i>	3	34	41	29	35	56	11	38

(continued)

Table I. (Continued)

Subcluster number	1.1	2.1	3.1	3.2	3.3	4.1	4.2	4.3
<i>Ligustrum vulgare</i>	18	33	38	42	30	11	35	34
<i>Galium sylvaticum</i> agg.	3	8	23	50	49	21	35	51
<i>Cruciata glabra</i>	3	52	3	34	37	25	22	57
<i>Mycelis muralis</i>	24	38	16	44	28	35	12	32
<i>Acer pseudoplatanus</i>	–	27	9	21	40	12	58	52
<i>Cardamine bulbifera</i>	27	25	34	15	21	35	26	29
<i>Carex pilosa</i>	–	–	38	44	28	23	14	30
<i>Aremonia agrimonoides</i>	39	42	14	21	44	–	5	8
<i>Campamula trachelium</i>	21	38	11	8	37	2	32	23
<i>Aegopodium podagraria</i>	6	22	20	6	21	26	49	19
<i>Cornus mas</i>	3	32	36	29	30	4	25	7
<i>Dryopteris filix-mas</i>	6	1	9	24	21	44	34	27
<i>Clematis vitalba</i>	27	41	12	15	19	–	28	9
<i>Veronica chamaedrys</i>	3	22	20	11	47	19	3	18
<i>Melittis melissophyllum</i>	–	22	11	27	33	–	15	18
<i>Tilia cordata</i>	–	2	11	18	9	25	37	15
<i>Dactylis glomerata</i>	12	22	14	26	30	2	3	3
<i>Milium effusum</i>	27	8	12	11	5	23	2	23
<i>Tilia platyphyllos</i>	12	9	12	21	23	4	20	10
<i>Ulmus glabra</i>	3	6	20	26	7	2	31	12
<i>Hieracium murorum</i>	15	26	–	2	12	16	5	29
<i>Sambucus nigra</i>	3	2	27	24	2	16	20	8

Note: Diagnostic species for the clusters and subclusters (defined as those with $\phi \geq 30$) are shown, ranked by decreasing value of the phi-coefficient, indicated by shadings (for clusters and subclusters) and asterisks (for subclusters).

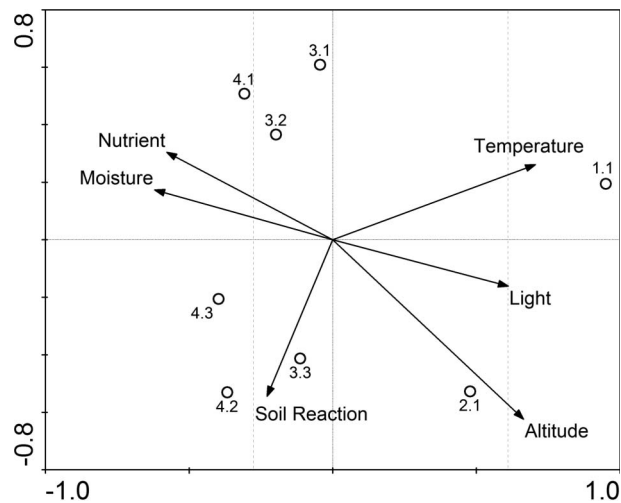


Figure 4. Passive projection of Pignatti indicator values and values of altitude onto the PCA diagram of eight subclusters. The subclusters are numbered as in Table I and Figure 2. Only indicator values with the highest correlations with the first two PCA axes are shown. The highest correlations with the first axis have the indicator values for temperature (0.7053), altitude (0.6641), moisture (-0.6198), light (0.6104) and nutrient (-0.5780), with the second axis the values for altitude (-0.6236) and soil reaction (-0.5444).

The main gradient that influences species composition in oak-hornbeam forests on the Apennines is the macroclimatic gradient north-south. Gradients on the Balkan peninsula are more complex. Besides the macroclimatic gradient north-south (northwest to southeast), continentality is also very important and also the presence of the mountain chains of the Alps and Balkans. Therefore oak-hornbeam forests on the Balkans are

more diverse and both Balkan groups (clusters) are further divided into three subgroups (subclusters).

We cannot find such a diversity in the Italian peninsula because it is very narrow and the continentality is evident only in a few mountain areas that are more complex in morphology, such as in the central Apennine areas (from the mountain chain of Sibillini to Gran Sasso).

Oak-hornbeam forests in the northwest Balkans are zonal vegetation, therefore the ecological diversity of these forests is higher than that towards the south of the Balkans, where this vegetation is azonal, and all diversity is due only to gradients of continentality and altitude. The northwestern Balkan and southern Alps forests are further divided by the TWINSPAN into three ecological groups: moist *Q. robur* group, basiphilous and moderate acidophilous group, while central-southern Balkan oak-hornbeam forests are separated into three phytogeographical groups: lowland pannonian, hilly pannonian and montane south-central Balkan.

In the northwest Balkans, in a more humid and cold climate, some *Q. robur* forests are classified as oak-hornbeam forests and are transitional towards the alliance *Alnion incanae*. Towards the south, because of the warmer and less humid climate, *Q. robur* forests develop only on very moist and overflowed soils and are therefore classified within alliance *Alnion incanae*.

Towards the south of the Balkans, where this type of vegetation is azonal, due to the warmer climate forests thrive on colder, acidic soils, at higher altitudes and also in shaded, moist and cold valleys at lower altitudes in the zone of *Q. frainetto* forests (Kojić et al. 1998).

In the Apennines, this type of vegetation extends far to the south of the peninsula (also including the Gargano peninsula), while in the Balkans only to the region of Macedonia, and there is no indication of the appearance of *Carpinus* forests in Greece (Raus 1980; Bergmeier 1990). The main reason is probably the different macroclimatic circumstances of the two peninsulas. The climate of the Apennines is – in comparison to the southern part of the Balkans – more oceanic or suboceanic with a higher amount of precipitation (Blasi et al. 2004), that enables the development of mesophilous oak-hornbeam forests also at lower altitudes, despite their geographical position in the south.

The lack of similarity between the Apennine and Balkan clusters, as indicated by the dendrogram and by the high number of differential species and lack of common species (Table I) between the Apennine and the Balkan oak-hornbeam forests, suggests a revision of the syntaxonomic position of oak-hornbeam forests of the Apennines separately from Balkan, southern Alps and padanian oak-hornbeam forests. On the other hand, numerical analysis has revealed a high similarity between northern- central and southern Apennine oak-hornbeam forests (clusters 1 and 2), which were traditionally classified into two different alliances. This similarity is also confirmed by the group of diagnostic species common for both groups of forests (Table I).

Therefore, the suballiance *Pulmonario apenninae-Carpinenion betuli*, traditionally classified into the alliance *Erythronio-Carpinion*, is now at our suggestion classified into the alliance *Physospermo verticillati-Quercion cerris* that comprises together forests of *Q. cerris* and *C. betulus* of the Apennines. The typical suballiance *Physospermo verticillati-Quercenion cerris* suball. nova, corresponds to the formations of the southern Apennines, as described in Biondi et al. (2008), while the suballiance *Pulmonario apenninae-Carpinenion betuli* comprises the central and northern Apennines formations. In Table I the characteristic and differential species of the two suballiances are brought into evidence.

Analyses support the classification of the northwestern and central-southern Balkan and southern Alps oak-hornbeam forests into the common alliance *Erythronio-Carpinion*. In this way, the classification of central-southern Balkan oak-hornbeam forests is solved, as these forests were traditionally classified into the provisional alliance *C. moesiacum*. Both alliances, Balkan and southern Alps alliance *Erythronio-Carpinion* and Apennines alliance *Physospermo verticillati-Quercion cerris*, are vicariants to the Central-European alliance *Carpinion betuli*. This is not the same pattern as used for some other types of vegetation (*Aremonio-Fagion*, *Ostryo-Tilienion*), where forests of the Apennines and Balkans were classified into the same alliance or suballiance vicariant to the central European alliance or suballiance. The reason for the lack of similarity between the Apennine and Balkan oak-hornbeam forests – and therefore different classification of these forests – could lie in the fact that these forests in the research area are anthropozoi-cally favored and that they are thriving on sites where dominant forests of the region, such as *F. sylvatica* forests and thermophilous *Q. cerris* and *Q. pubescens* forests, cannot develop. These sites seem to be considerably different between both peninsulas.

The traditionally phytogeographically defined suballiances *Lonicero-Carpinenion betuli*, *Erythronio-Carpinenion* and *Asparago tenuifolii-Carpinenion* were not distinguished by numerical analysis, and were therefore joined together into one phytogeographically wider defined suballiance *Lonicero-Carpinenion betuli* comprising oak-hornbeam forests of the northwestern Balkan and southern Alps, within which the forests are divided ecologically into three groups. For the central-southern Balkan oak-hornbeam forests we propose a new suballiance *Aceri tatarici-Carpinenion*.

Concerning all these facts and the numerical analyses carried out in this research, we propose the following syntaxonomy of the oak-hornbeam forests of southeastern Europe:

Proposed syntaxonomic scheme

Class: *Querc-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937

Order: *Fagetalia sylvaticae* Pawłowski et al. 1928

Alliance: *Physospermo verticillati-Quercion cerris* Biondi et al. 2008

Suballiance: *Physospermo verticillati-Quercenion cerris* Biondi et Casavecchia in Košir et al. suball. nova hoc loco (cluster 1 in Table I)

Suballiance: *Pulmonario apenninae-Carpinenion betuli* Biondi et al. 2002 (cluster 2 in Table I)

Alliance: *Erythronio-Carpinenion betuli* (Horváth 1938)

Marinček in Wallnöfer, Mucina et Grass 1993 (clusters 2, 3 and 4 in Table I)

Suballiance: *Aceri tatarici-Carpinenion betuli* Košir et al. all nova hoc loco (cluster 3 in Table I) (incl. *C. moesiacum*)

Group of lowland pannonian associations (subcluster 3.1 in Table I)

Group of hilly pannonian associations (subcluster 3.2 in Table I)

Group of montane central-south Balkan forests (subcluster 3.3 in Table I)

Suballiance: *Lonicero caprifoliae-Carpinenion betuli* Vukelić in Marinček 1994 (cluster 4 in Table I) (incl. *Asparago tenuifolii-Carpinenion betuli* Marinček & Poldini 1994, *Erythronio-Carpinenion betuli* Marinček 1994)

Group of *Quercus robur* associations (subcluster 4.1 in Table I)

Group of basiphilous associations on carbonate bedrock in the pre-Alpine and submediterranean region (subcluster 4.2 in Table I)

Group of neutrophilous-moderate acidophilous associations mostly on noncarbonate bedrock in pre-Dinaric and subpannonian region (subcluster 4.3 in Table I)

The holotypus of the *Physospermo verticillati-Quercenion cerris* is the association *Physospermo verticillati-Quercetum cerris* Aita et al. 1977 em Ubaldi et al. 1987 holotypus hoc loco.

The holotypus of the *Aceri tatarici-Carpinenion betuli* is the association *Asperulo taurinae-Carpinetum betuli* Kevey in Borhidi 1998 holotypus hoc loco.

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References

- Bennett KD, Tzedakis C, Willis KJ. 1991. Quaternary refugia of north European trees. *J Biogeogr* 18: 103–115.
- Bergmeier E. 1990. Wälder und Gebüsche des Niederen Olymp (Káto Olimbos, NO-Thessalien). Ein Beitrag zur systematischen und orographischen Vegetationsgliederung Griechenlands. *Phytocoenologia* 18: 161–342.
- Bergmeier E, Dimopoulos P. 2001. *Fagus sylvatica* forest vegetation in Greece: Syntaxonomy and gradient analysis. *J Veg Sci* 12: 109–126.
- Biondi E. 2011. Phytosociology today: methodological and conceptual evolution. *Plant Biosyst* 145 Supplement: 19–29.
- Biondi E, Allegrezza M, Casavecchia S, Pesaresi S, Vagge I. 2006. Lineamenti vegetazionali e paesaggio vegetale dell'Appennino centrale e settentrionale. *Biogeographia* XXVII: 35–129.
- Biondi E, Blasi C, Burrascano S, Casavecchia S, Copiz R, Del Vico E, et al. 2009. Italian interpretation manual of the habitats (92/43/EEC Directive). Ministero dell'Ambiente e della Tutela del Territorio e del Mare. Available: <http://vnr.unipg.it/habitat/> Accessed Aug 2012 13.
- Biondi E, Casavecchia S, Biscotti N. 2008. Forest biodiversity of the Gargano Peninsula and a critical revision of the syntaxonomy of the mesophilous woods of southern Italy. *Fitosociologia* 45: 93–127.
- Biondi E, Casavecchia S, Pesaresi S. 2010. Interpretation and management of the forest habitats of the Italian peninsula. *Acta Botanica Gallica* 157: 687–719.
- Biondi E, Casavecchia S, Pesaresi S. 2011. Phytosociological synrelevés and plant landscape mapping: From theory to practice. *Plant Biosyst* 145: 261–273.
- Biondi E, Casavecchia S, Pesaresi S, Zivkovic L. 2012. Natura 2000 and the Pan-European Ecological Network: A new methodology for data integration. *Biodiver Conserv* 21: 1741–1754.
- Biondi E, Casavecchia S, Pinzi M, Allegrezza M, Baldoni M. 2002. The syntaxonomy of the mesophilous woods of the Central and Northern Apennines (Italy). *Fitosociologia* 39: 71–93.
- Blasi C, Biondi E, Izco J. 2011. 100 years of plant sociology: A celebration. *Plant Biosyst* 145 Supplement: 1–3.
- Blasi C, Di Pietro R, Filesi L. 2004. Syntaxonomical revision of *Quercetalia pubesceti-petraeae* in the Italian Peninsula. *Fitosociologia* 41: 87–164.
- Blasi C, Frondoni R. 2011. Modern perspectives for plant sociology: The case of ecological land classification and the ecoregions of Italy. *Plant Biosyst* 145 Supplement: 30–37.
- Blasi C, Marchetti M, Chiavetta U, Aleffi M, Audisio P, Azzella MM, et al. 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosyst* 144: 160–170.
- Bohn U, Gollub G, Hettwer C, Neuhäuslová Z, Schlüter H, Weber H. 2003. Karte der natürlichen Vegetation Europas. Erläuterungstext. Bundesamt für Naturschutz, Bonn.
- Braun-Blanquet J. 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde. 3rd ed. Wien, NY: Springer.
- Bruehlheide H. 1995. Die Grünlandgesellschaften des Harzes und ihre Standortsbedingungen. Mit einem Beitrag zum Gliederungsprinzip auf der Basis von statistisch ermittelten Artengruppen. *Diss Bot* 244: 1–338.
- Bruehlheide H. 2000. A new measure of fidelity and its application to defining species groups. *J Veg Sci* 11: 167–178.
- Chytrý M, Tichý L, Holt J, Botta-Dukát Z. 2002. Determination of diagnostic species with statistical fidelity measures. *J Veg Sci* 13: 79–90.

- Čarni A, Košir P, Karadžić B, Matevski V, Redžić S, Škvorc Ž. 2009. Thermophilous deciduous forests in Southeastern Europe. *Plant Biosystems* 143: 1–13.
- Council of Europe. 1996. The Pan-European biological and landscape diversity strategy, a vision for Europe's natural heritage. Strasbourg, France: Council of Europe.
- Diaci J, Rozenbergar D, Boncina A. 2010. Stand dynamics of Dinaric old-growth forests in Slovenia: Are indirect human influences relevant? *Plant Biosyst* 144: 194–201.
- Di Pietro R, Izco J, Blasi C. 2004. Contribution to the nomenclatural knowledge of *Fagus sylvatica* woodlands of southern Italy. *Plant Biosystems* 138: 27–36.
- Dzwonko Z, Loster S. 2000. Syntaxonomy and phytogeographical differentiation of the *Fagus* woods in the Southwest Balkan Peninsula. *J Veg Sci* 11: 667–678.
- Dzwonko Z, Loster S, Dubiel E, Drenkovski R. 1999. Syntaxonomic analysis of beechwoods in Macedonia (former Republic of Yugoslavia). *Phytocoenologia* 29: 153–175.
- European Commission. 2007. Interpretation manual of European Union habitats. Eur 27. 142 pp. DG Environment. Available: http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/2007_07_im.pdf. Accessed Aug 2012 24.
- Feoli E, Ganis P, Venanzoni R, Zuccarello V. 2011. Toward a framework of integrated knowledge of terrestrial vegetation system: the role of databases of phytosociological relevés. *Plant Biosyst* 145 Supplement: 74–84.
- Géhu JM. 2011. On the opportunity to celebrate the centenary of modern phytosociology in 2010. *Plant Biosyst* 145 Supplement: 4–8.
- Gömöry D, Paule L, Brus R, Zhelev P, Tomović Z, Gračan J. 1999. Genetic differentiation and phylogeny of beech on the Balkan peninsula. *J Evol Biol* 12: 746–754.
- Hennekens SM, Schaminée JHJ. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *J Veg Sci* 12: 589–591.
- Hill MO. 1979. TWINSpan – A Fortran program for arranging multivariate data in an ordered two way table by classification of the individuals and the attributes. Ithaca, NY: Department of Ecology and Systematics, Cornell University.
- Horváth F, Bidló A, Heil B, Király G, Kovács G, Mányoki G, et al. 2012. Abandonment status and long-term monitoring of strict forest reserves in the Pannonian biogeographical region. *Plant Biosyst* 146: 189–200.
- Knollová I, Chytrý M. 2004. Oak-hornbeam forests of the Czech Republic: Geographical and ecological approaches to vegetation classification. *Preslia* 76: 291–311.
- Knollová I, Chytrý M, Tichý L, Hájek O. 2005. Stratified resampling of phytosociological databases: Some strategies for obtaining more representative data sets for classification studies. *J Veg Sci* 16: 479–486.
- Kojić M, Popović R, Karadžić B. 1998. Sintaksonomski pregled vegetacije Srbije. Institut za biološka istraživanja »Siniša Stanković«, Beograd.
- Košir P, Čarni A, Di Pietro R. 2008. Classification and phytogeographical differentiation of broad-leaved ravine forests in southeastern Europe. *J Veg Sci* 19: 331–342.
- Magri D. 1998. Quaternary history of *Fagus* in the Italian peninsula. *Ann Bot (Roma)* 56: 147–154.
- Marinček L, Čarni A. 2000. Die Unterverbände der Hainbuchenwälder des Verbandes *Erythronio-Carpinion betuli* (Horváth 1938) Marinček in Wallnöfer, Mucina et Grass 1993. *Scopelia* 45: 1–20.
- McCune B, Grace JB. 2002. Analysis of ecological communities. Glenden Beach, OR: MjM Software Design.
- Oberdorfer E. 1992. Süddeutsche Pflanzengesellschaften. Wälder und Gebüsche. Gustav Fischer Verlag, Jena.
- Petit RJ, Brewer S, Bordács S, Burg K, Cheddadi R, Coart E, et al. 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecol Manage* 156: 49–74.
- Pignatti S, Menegoni P, Pietrosanti S. 2005. Valori di bioindicazione delle piante vascolari della flora d'Italia. *Braun-Blanquetia* 39: 1–97.
- Pott R. 2011. Phytosociology: A modern geobotanical method. *Plant Biosyst* 145 Supplement: 9–18.
- Raus T. 1980. Die Vegetation Ostthessaliens (Griechenland). III. *Quercus-Fagetia* und azonale Gehölzgesellschafte. *Bot Jahrb Syst* 101: 313–361.
- Rivas-Martinez S, Rivas-Saenz S. 1996–2009. Worldwide bioclimatic classification system. Spain: Phytosociological Research Center. Available: <http://www.globalbioclimatics.org> Accessed Aug 2012 13.
- Roleček J, Tichý L, Zelený D, Chytrý M. 2009. Modified TWINSpan classification in which the hierarchy respects cluster heterogeneity. *J Veg Sci* 20: 596–602.
- Schaminée JHJ, Janssen JAM, Hennekens SM, Ozinga WA. 2011. Large vegetation databases and information systems: new instruments for ecological research, nature conservation and policy making. *Plant Biosyst* 145 Supplement: 85–90.
- STATSOFT inc. 2007. STATISTIKA (data analysis software system), version 8.0. Available: www.statsoft.com Accessed Aug 2012 13.
- Škvorc Ž, Franjić J, Idžojtić M. 2005. Population structure of *Quercus pubescens* Willd. (*Fagaceae*) in Croatia according to morphology of leaves. *Acta Bot Hung* 47: 193–206.
- Ter Braak JFC, Šmilauer P. 2002. CANOCO Reference manual and CanoDraw for Windows user's guide. Software for canonical community ordination (version 4.5). Ithaca, NY: Microcomputer Power.
- Tichý L. 2002. JUICE, software for vegetation classification. *J Veg Sci* 13: 451–453.
- Tichý L, Chytrý M. 2006. Statistical determination of diagnostic species for site groups of unequal size. *J Veg Sci* 17: 809–818.
- Trinajstić I. 1992. A contribution to the phytogeographical classification of the Illyrian floral element. *Acta Bot Croat* 51: 135–142.
- Tsiripidis I, Bergmeier E, Dimopoulos P. 2007. Geographical and ecological differentiation in Greek *Fagus* forest vegetation. *J Veg Sci* 18: 743–750.
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, et al., editors. 1964–1980. *Flora Europaea*. Volume 1–5. Cambridge: Cambridge University Press.
- Tzedakis PC. 1993. Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* 364: 437–440.
- Tzonev R, Dimitrov M, Chytrý M, Roussakova V, Dimova D, Gussev C, et al. 2006. Beech forest communities in Bulgaria. *Phytocoenologia* 36: 247–279.
- Ubaldi D. 2003. La vegetazione boschiva d'Italia: Manuale di Fitosociologia forestale. Clueb, Bologna.
- Willner W, Grabherr G. 2007. Die Wälder und Gebüsche Österreichs. Spektrum, Akademischer Verlag.